THE CUTICULA AND SUBCUTICULA OF TRE-
MATODES AND CESTODES

PROFESSOR HENRY S. PRATT

HAVERFORD COLLEGE

THE membrane which forms the outer covering of the body of trematodes and cestodes and is usually called the cuticula differs in certain important particulars from that of other invertebrates, and its morphological significance has long been a matter of dispute. The most noticeable feature of this difference is the apparent lack of a hypodermis in these worms, the cuticula being bounded on its inner surface by the superficial muscle layers and the parenchyma which fills the body-cavity.

In the last few years, however, a theory of the cuticula, which in the early years of modern helminthology was the prevailing one, has been revived by Professor F. Blochmann (1896), who has presented its claims to recognition with so much force and ability that it has been accepted by most helminthologists and zoologists as best accounting for the facts. It has also found its way into some of the best text-books and bids fair to become, in the ordinary course of events, one of the dogmas of science.

According to this theory, the cuticula of trematodes and cestodes is a true cuticula morphologically, which is secreted by a hypodermis, as in other invertebrates. This hypodermis, however, has undergone a metamorphosis, for instead of forming a continuous layer of cells situated

705

immediately beneath the cuticula, it has dropped back of some or all of the superficial muscle layers into the parenchyma, its constituent cells have become more or less separated from one another, and it forms the broken or irregular tissue called the subcuticula.
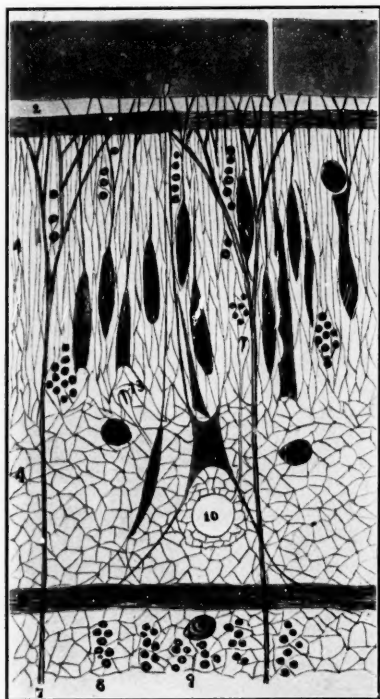
Fig. 1, which is taken from Blochmann's paper and ap-

Fig. 1. Transverse section from Ligula, a cestode (after Blochmann). 1, cuticula; 2, basal membrane; 3, circular muscles; 4, parenchyma; 5, subcuticular cells; 6, nerve; 7, dorsoventral muscles; 8, longitudinal muscles; 9, calcareous body; 10, excretory canal; 11, sense-cell; 12, myoblast; 13, flame-cell; 14, gland-cell; 15, sense-organ.

pears also in Claus and Grobben's "Lehrbuch," Braun's "Menschliche Parasiten" and Lankester's "Zoology," represents a section of the body-wall of a cestode (Ligula) and shows the relation of the cuticula to the subcuticular

cells as conceived by Blochmann and adopted by the au-
thors of these text-books.

Fig. 2 from Hein (1904), who follows Blochmann
closely, shows the same relations in the digenetic trema-
todes. It will be seen in both these figures that the sub-
cuticular cells form a distinct although irregular layer
and are joined with the inner surface of the cuticula by
long projections. These Blochmann and Hein regard as
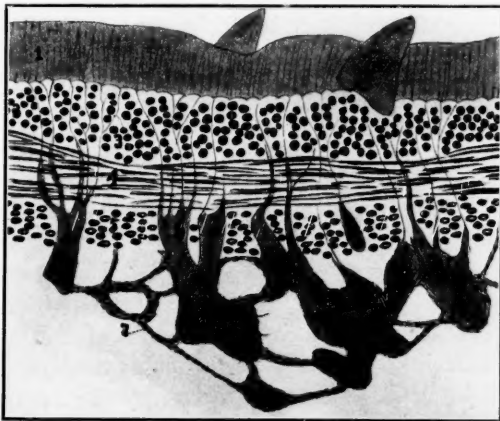the ducts through which formative material is added to

Fig. 2. Longitudinal section from *Fasciola hepatica*, a digenetic trematode
(after Hein). 1, cuticula; 2, spine; 3, circular muscles; 4, longitudinal muscles;
5, oblique muscles; 6, subcuticular cells; 7, parenchyma.

the cuticula, of which these cells are thus the matrix. It
will further be noticed in these figures that the sub-
cuticular cells apparently do not form a part of the paren-
chyma in which they lie, and also that among them are
sense cells and gland cells which are usually conceded to
have an epithelial origin.

Another theory of the cuticula which is not very differ-
ent from Blochmann's is that of Brandes (1892), who
also considers the structure in question to be the product
of the subcuticular cells (Fig. 3). These, however, he
conceives to be single-celled glands which are joined with

the cuticula by means of ducts passing between the super-
ficial muscle fibers. Brandes's theory is based upon an
examination of a considerable number of monogenetic
and digenetic trematodes, in both of which groups he finds
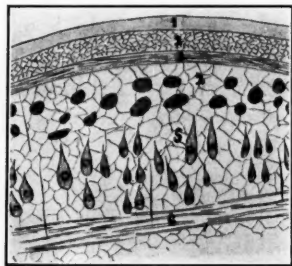practically identical structural conditions in the cuticular
and subcuticular layers. His
drawings, however, are very
diagrammatic. The subcuticu-
lar cells certainly do not exist
in any trematodes in the form
in which he shows them, and
those in his figures of mono-
genetic trematodes are not the
subcuticular cells at all, but the
single-celled glands which are
present at the forward end of
most of these worms.

Fig. 3.   Transverse section
from *Onchocotyle appendiculata,*
a monogenetic trematode (after
Brandes). 1, cuticula; 2, paren-
chyma; 3, circular muscles; 4,
longitudinal muscles; 5, subcu-
ticular cells; 6, oblique muscles.

Tennent (1906) and others
have adopted Brandes's view.
It will at once be noted that the
main difference between his theory and that of Blochmann
lies in their interpretation of the subcuticular cells, the
former holding them to constitute a hypodermis and to be
consequently an epithelium of ectodermic origin, the latter
considering them simple gland cells which are derivatives
of the parenchyma.

These important theories, although they may seem to
account for the facts in the animals investigated and to
place the whole matter upon a substantial logical basis,
have, however, met with considerable opposition, and, it
seems to me, are not well grounded. It is quite evident
that if they are true they must have universal applica-
tion. If the subcuticular cells are the matrix of the cuti-
cula, whether we consider them to be single-celled glands
or the constituent parts of a hypodermis, then they must
be present in all trematodes and cestodes, since this pecul-
iar cuticula characterizes all of these worms (with the

exception of the Temnocephalidæ) from their early larval stages to those of the adult.

But this is far from being the case. The subcuticular cells are wanting in probably the whole group of monogenetic trematodes, also in most of the Aspidobothridæ and in certain other digenetic trematodes. Goto (1894, 1899) has made a careful anatomical study of over forty species of monogenetic trematodes belonging to some sixteen genera, and has found no subcuticular cells in any
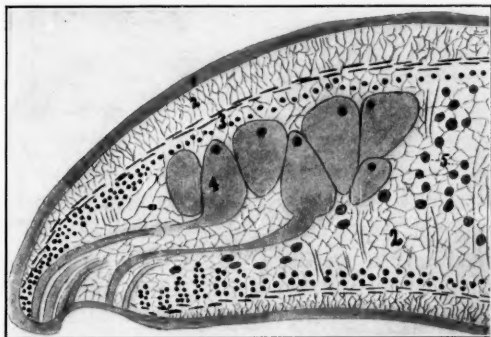

FIG. 4.   Transverse section from *Dionchus agassizi*, a monogenetic trematode (after Goto).   1, cuticula ; 2, parenchyma ; 3, muscles ; 4, single-celled glands ; 5, parenchyma nuclei.

of them (Fig. 4). He directed his attention specially to the discovery of these cells in the worms studied by Brandes, but says :

Although I directed my special attention to the point, I have utterly failed to observe those subcuticular cells so beautifully drawn by Brandes in his figures in the very same genera that he describes.

Cerfontaine (1899) has also made a study of some twenty-eight species of monogenetic trematodes with the same result (Fig. 5).

It is true that peripheral single-celled glands are present in probably all of these worms, the ducts of which can be easily seen (Figs. 1 and 4) to pass not merely to but through the cuticula to the outside surface of the body. These gland cells are usually grouped at the forward end

of the body or in the neighborhood of the suckers, and are variously interpreted as sticky or mucous glands or as irritants to increase the flow of the juices which serve as the food of the worm. They do not extend over the whole body or any large part of it, and are not the subcuticular

FIG. 5. Longitudinal section from *Squalonchocotyle vulgaris,* a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, parenchyma; 3, circular muscles; 4, longitudinal muscles; 5, parenchyma nuclei.

cells, nor are they so considered by any authors who have studied them. They also differ markedly in shape from the subcuticular cells, being more or less pear-shaped and regular in outline, each cell having a distinct and single
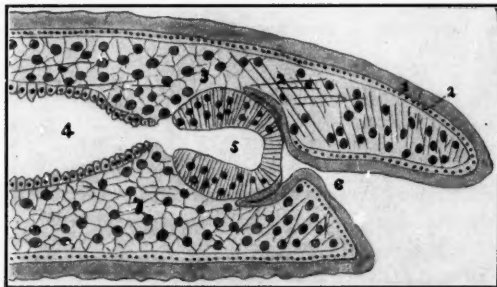

FIG. 6. Longitudinal section from *Stichocotyle nephropis,* an aspidobothrid (after Nickerson). 1, cuticula; 2, muscles; 3, parenchyma; 4, intestine; 5, pharynx; 6, mouth; 7, parenchyma nuclei.

duct of large size. The subcuticular cells, on the other hand, are often irregular in shape, often anastomosing with one another and in many cases having the appearance of parenchyma cells. They also show no ducts at all,

but in many forms are connected with the cuticula by branched or anastomosing processes (Figs. 1 and 2) which are interpreted by many to be ducts.

The lack of subcuticular cells in Aspidobothridæ has been shown by Monticelli (1892) and Nickerson (1902) for Cotylogaster, Nickerson (1894) for Stichocotyle (Fig. 6), and Osborn (1904) for Cotylaspis. Single-celled glands are, however, present in all these worms.

In the other digenetic trematodes and in cestodes, also, although subcuticular cells have been shown to be present in most of the forms whose finer structure is known, it is certain that some do not possess them. In *Distomum palliatum* and *Distomum reticulatum,* for instance, Looss (1885) found none of them, and in *Hemiurus crenatus* and *Gasterostomum gracilescens* Lander (1904) and Tennent (1906), respectively, found them only in very small numbers. In all digenetic trematodes and cestodes, also, it can very often be shown that the cells in question bear no adequate relation to the cuticula beneath which they lie. Thus they are present sometimes in certain parts of the body only, as has been shown in my study of Apoblema (1898), in which the appendix of the youthful distome, although covered with exactly the same cuticula as in the rest of the body, is entirely without subcuticular cells. The suckers, also, in cestodes and the tail of the cercaria have none of these cells, although they possess a cuticula.

In many digenetic trematodes, too, the subcuticular cells, although present, are entirely too few in number to produce the thick cuticula present, as shown in *Hemiurus crenatus* (Fig. 7) by Lander, and in numerous other cases. It must be remembered in this connection that the cuticula of trematodes and cestodes is probably at all times a growing tissue, which is constantly being renewed on its inner surface in proportion as it wears away on its outer, so that if the subcuticular cells are its matrix they should be equally present in all parts of the body and at all times of the animal's active life.

In many digenetic trematodes the cuticula is not of
equal thickness on all parts of the body and these varia-
tions in thickness are not correlated with corresponding
differences in the subcuticular cells beneath them.   For
instance, the cuticula of the appendiculate distomes has
numerous transverse rings which give a longitudinal sec-
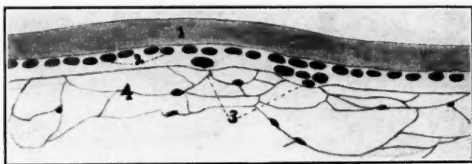tion a serrated appearance.   These rings are due solely to

Fig. 7.   Transverse section from *Hemiurus crenatus,* an appendiculate dis-
tome (after Lander).   1, cuticula ; 2, longitudinal muscles ; 3, subcuticular cells ;
4, parenchyma.

variations in the thickness of the cuticula, the inner sur-
face of it being quite smooth, and we might expect the
subcuticular cells, if they secreted the cuticular, to be
larger or more numerous beneath the rings.   This is, how-
ever, not the case, these cells showing no variations what-
ever beneath these cuticular rings.

The relations of the spines, hooks, scales and other
special cuticular structures to the subcuticular cells also
furnish an argument against the epithelial or glandular
nature of the latter.   These spines and hooks are of very
common occurrence and are often very prominent objects
in trematodes and cestodes, their function usually being
to aid in anchoring the parasite to its host.   They are
seen in their simplest form in the digenetic trematodes,
(Fig. 2) in which they usually appear as specialized parts
of the cuticula.   In the monogenetic trematodes and the
cestodes, on the other hand, they are often of huge size
and of more or less complex structure and may extend be-
neath the cuticula among the muscles and the parenchyma
cells.

That these organs are similar in essential structure and

in origin to the cuticula has been very well shown by Looss (1894), Young (1908) and other authors, who have traced their development and growth.

If now the cuticula is the product of the underlying subcuticular cells, we should expect to find some special development of them beneath the hooks and spines, especially where these are very large, just as in the integument of insects a cuticular hair or scale is invariably situated over the enlarged hypodermal cell which produces it. Nothing of the sort exists, however, in trematodes and cestodes. The subcuticular cells beneath the hooks and spines do not differ in size, number or arrangement from the adjacent cells, and in the monogenetic trematodes, which are often provided with gigantic hooks, no subcuticular cells at all are present. In the six-hooked embryo of cestodes the hooks make their appearance in the embryonic parenchyma, while there are as yet no subcuticular cells present. The parenchyma is thus the matrix of the hooks at this early stage of the animal's existence.

Another point of importance is the essential difference in structure between the cuticula of trematodes and cestodes and that of other worms and of arthropods in which the cuticula is the secretion of an undoubted hypodermis. In the former the characteristic lamellate structure of a

8   9
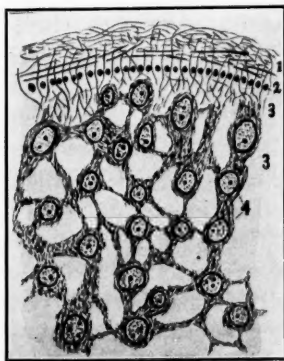
Fig. 8. Section of wall of young cysticercus of *Tænia serrata* (after Young). 1, cuticula; 2, muscles; 3, parenchyma; 4, parenchyma nuclei.

Fig. 9. Section of body wall of *Squalonchocotyle vulgaris*, a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, nuclei in the cuticula; 3, parenchyma; 4, muscles.

typical arthropod or worm cuticula is never present (although it may be made up of several layers), but, on the other hand, a fundamentally fibrous structure can often be demonstrated with perfect clearness, the fibers being sometimes in very evident connection with the parenchyma beneath and a portion of it (Figs. 8 and 9).

In fact, the so-called ducts of the subcuticular cells are nothing more nor less than the fibrous projections of these cells which, together with similar projections of the parenchyma cells themselves, sometimes extend to, and occasionally, especially in young animals, into the cuticula. In certain cases these fibers may arrange themselves so as to form a series of vertical strands in the cuticula, passing between its inner and outer surfaces, and have been interpreted in the past to be pore-canals, structures which are probably not present in any trematodes or cestodes. Whatever toughness of texture the cuticula of these worms possesses is probably due to this fundamentally fibrous or leathery structure. The cuticula is further exceedingly elastic; it is often very soft or even semi-fluid and easily destroyed in caustic potash and as the result of maceration; and it is never moulted as a whole nor can it be usually separated from the tissues beneath—all of which characteristics are foreign to the cuticula of other worms and of arthropods.

The differences between an undoubted hypodermis and the subcuticular cells are also fundamental and very striking, and are not satisfactorily explained by Blochmann, who compares with them the hypodermal cells of Hirudo and other animals which may be more or less separated from one another by parenchyma and other tissues. The origin of these cells forms the embryonic parenchyma, as shown clearly by many authors, and the frequent anastomosing of them with one another and with the surrounding parenchyma, are characters which no hypodermis possesses.

It is true that there is a strong superficial resemblance between the subcuticular cells in cestodes—but seldom or

never in trematodes—and epithelial cells, without which it
is not likely that any one would ever have thought of this
epithelial theory. These cells in cestodes are, as we have
seen, usually elongated and spindle-shaped and lie paral-
lel to one another, so that they look a good deal like iso-
lated epithelial cells. But it must also be noticed (Fig.
1) that all the other cellular elements of the peripheral
region—the parenchyma cells, the gland cells and the
sense cells—are also elongated and spindle-shaped and lie
parallel to one another and to the subcuticular cells. Ap-

Fig. 10.   Golgi section from a cestode (Ligula) showing the branched in-
sertion of the dorsoventral muscles in the cuticula (after Zernecke). 1, cuticula ;
2, the muscles ; 3, sense-organ ; 4, nerves ; 5, sense-cell.

parently some common cause, in the nature of a tension
in a dorsoventral direction, has acted upon the entire
peripheral region of the body of the worm, distorting
more or less all the structures in it. Leuckart (1886) has
suggested—and Leuckart's suggestions are always fruit-
ful—that this spindle form is due to the action of the
powerful dorsoventral muscles which run across the

proglottid and are inserted in the cuticula of each surface by numerous branching strands (Fig. 10). He even thought that the spindle cells might be the tendons of these muscles, which, however, is not the case, since Zernicke (1895) and others have demonstrated the branched insertions just mentioned. It is my opinion, however, that it is the pull of these muscles and especially of their branched insertions which interweave themselves among all the peripheral tissues of the body (Fig. 10), which has thus distorted all the cellular elements in this region and caused them to assume their characteristic shape and appearance. And this opinion is confirmed by the fact that in the scolex and between the proglottids, where these muscles are weak or absent, the subcuticular cells are not spindle-shaped, but have the form of ordinary parenchyma cells (Leuckart).

The embryological and larval history of these worms also furnishes arguments against the epithelial theory. The cuticula comes into existence, both in trematodes and cestodes, before the subcuticular cells have differentiated and grows independently of them (Figs. 8 and 11). Its early growth has been well described by Looss for trematodes in Diplodiscus (1892) and in a considerable number of distomes (1894) and by Roewer (1906) in distomes, and for cestodes by Young (1908) in *Cysticercus pisiformis*. These authors show also very conclusively that when the subcuticular cells do finally make their appearance it is as differentiations of the embryonic parenchyma cells and that at no time is anything like an epithelium present in the position in which they are found (Fig. 8).

The moulting of the outer epithelium (ectoderm) in larval trematodes and cestodes has also an important bearing upon this question, inasmuch as in consequence of it the adult worm is entirely composed of tissues derived primarily from the interior embryonic cell mass (endoderm or mesenchyme). The subcuticular cells can not consequently be of ectodermal origin and can not be

homologous to the hypodermis of other invertebrates. In trematodes this moulting may occur in each of the larval stages. It has been directly observed in the mirácidium many times, among others by both Thomas (1883) and Leuckart (1886) who saw the miracidium of *Fasciola hepatica* shed its ciliated ectoderm when it entered the liver of *Lymnæa trunculata*. In the redia and cercaria stages it has also been directly observed by a number of investigators. Looss has made the most complete record of his observations. He (1892, 1893, 1894, also Braun, 1893, p. 818) has seen both the redia and cercaria shed its outer epithelium in about a dozen species of distomes, as just remarked, after which procedure the young worm was covered with the definitive cuticula. This Looss considers the product of secretions of the entire body of the parenchyma.

Although the cercaria has thus been seen to shed its peripheral epithelium, there have been recorded a number of cases where it is not shed all at one time, portions remaining until the cercaria is fully grown or nearly so. The appendiculate distome I described some time ago (1898) was a good example of this procedure. The appendix of the young worm in this case retained its cercarian ectoderm although the male genital organs were mature and spermatozoa were being produced. The remainder of the body was without an epithelium, but was covered by the characteristic cuticula, which was also present beneath the epithelium on the appendix. This epithelium was soon after moulted and then the outer covering of the appendix was exactly similar to that of the rest of the body.

In cestodes the early stages of development are very similar to those of trematodes, the ectoderm having been observed by Schauinsland (1885), Leuckart (1886) and others to be moulted in exactly the same way. It is the opinion of many students of cestodes, however, that the stage in which an outer epithelium is present is passed over in most of these animals. The young worms thus

never have an outer epithelium, but the characteristic cuticula is their earliest body-covering.

Although there can be no doubt that the outer epithelium of trematode and cestode embryos and larvæ is often, perhaps usually, moulted, it must be mentioned that cases have also been recorded in which no such moulting has apparently taken place. Schauinsland (1883) has shown that in the embryo of *Distomum tereticolle*, the ectoderm gradually loses its cell boundaries and nuclei and becomes metamorphosed into a cuticula. A similar process has been described by Leuckart (1886) in the young redia of *Fasciola hepatica*, by Zeller (1872) in the embryo of Polystoma, and by other authors.

These facts and others which will be mentioned have led many helminthologists to subscribe to a third theory of the cuticula of trematodes and cestodes—that which sees in it a metamorphosed or cuticularized epithelium (ectoderm). This is one of the oldest of the theories relating to the cuticula, having been first proposed by Wagener in 1855, and in later years having such able supporters as Monticelli, Goto, Nickerson and Braun, although the last named has apparently abandoned it in favor of Blochmann's theory. It is based mainly upon the facts that embryonic and larval ectoderms have been observed in a degenerate condition as just stated, and also that frequently nuclei are found imbedded in the adult cuticula. These nuclei are sometimes well formed (Fig. 12), but often have the appearance of being in a more or less broken-down condition and to be degenerating. Open spaces and vesicles are also often present in the cuticula.

FIG. 11. Section of wall of a young cysticercus of *Tænia serrata* (after Young). 1, cuticula; 2, parenchyma.

Much has been observed which supports this theory. Braun (1893, p. 590) found numerous oval nuclei in the cuticula of *Monostomum mutabile*, Maclaren (1905) found

them in Distomum sp. (Fig. 12), Monticelli (1892, 1894)
in a number of trematodes, Nickerson (1902) in Cotylo-
gaster, Cerfontaine (1899) in *Squalonchocotyle vulgaris*
(Fig. 9) : many other authors also have seen and de-
scribed them. There can be no doubt that however one
may interpret the alleged cuticularization of the embry-
onic and larval ectoderms,—and Brandes, Looss, Braun
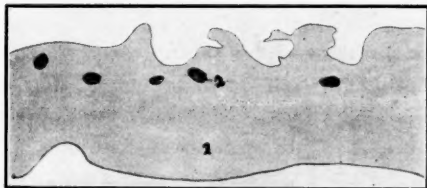and others will not admit that it has been demonstrated,

FIG. 12.   Section of the cuticula of a distome containing nuclei (after Mac-
laren).   1, cuticula ; 2, nucleus imbedded in cuticula.

—nuclei or nuclei-like bodies occasionally appear in the
cuticula of both larval and adult trematodes and cestodes.
These have been variously interpreted by different au-
thors.   Blochmann (1896), for instance, asserts that they
are the end organs of sense cells which are imbedded in
the cuticula, while Looss (1893) thinks they may be por-
tions of formed material in the act of passing from the
parenchyma into the cuticula.

It seems to me that the occurrence of nuclei in the
cuticula has been recorded by too many competent ob-
servers to be explained away in any such manner.   They
undoubtedly do occasionally occur, being either nuclei
which are parts of a degenerating epithelium or perhaps
those which belong to the peripheral portion of the paren-
chyma and have become enclosed in the rapidly forming
and growing cuticula.   This last probability is strength-
ened by the observation of Maclaren (1905) and others
that such nuclei occur most frequently in the cuticula of
young worms, and by those of Young (1908) and Cer-
fontaine (1899) who show, respectively, that the cuticula

of the very young larva is composed essentially of fibers
and nuclei closely bound together (Fig. 11) and that the
adult cuticula may be in direct connection with the sub-
jacent parenchyma and contain some of its nuclei (Fig.
9). It is conceivable, however, notwithstanding these
facts, that foreign objects such as particles of coagulated
blood, which often adheres to the outer surface of these
worms, could be forced into the soft cuticula from the
outside as a result of the pressure to which the worms are
often subjected in their natural environment, or perhaps
in the compressor or under the cover-glass of the investi-
gator, and thus appear like degenerating nuclei in it.
The vesicles, which often appear in the cuticle, are prob-
ably artefacts due to the influence of reagents on the soft
cuticula of a dying or a compressed animal. The cuticula
also macerates very rapidly, in fact it is often the first
part of the body to show death-changes, and may easily
become vesicular by the passage of fluids or gases into it
from the parenchyma or from the outside.

In my own opinion this theory of the metamorphosed
epithelium breaks down, at least as a universal theory,
for several reasons. In the first place, the outer epi-
thelium is undoubtedly moulted in very many larval
trematodes, as has been observed by many competent
observers, and a worm can not both shed its epithelium
and still enjoy the possession of it, even in a modified
form. The theory can not thus have general application.
In the second place, even if the ectoderm of the embryo or
larva is cuticularized in certain cases, as has been ob-
served, the cuticula of the adult worm is not yet accounted
for, as the worm increases in size many-fold, often many
thousand-fold, while growing from the larval to the adult
condition. In other words, the cuticula of the mature
worm may be quite a different structure from that of the
larva, and if it is true that the cuticula of the larva is a
metamorphosed epithelium, then that of the adult is
formed of a different material and in a different way. In-
asmuch as the cuticula is constantly growing on its inner

surface and being flaked off on its outer, it is not a struc-
ture which is formed once for all but one which depends
on a more or less uniform secretion from the tissues
beneath.

What then is the morphological significance of the cuti-
cula of trematodes and cestodes if it is neither a meta-
morphosed epithelium nor the product of an underlying
hypodermis or of single-celled glands. I believe that it is
the peripheral portion of the parenchyma which forms the
outer coating of the body after the disappearance of the
larval epithelium (ectoderm), and which has been solidi-
fied into a thick membrane by the secretion of cuticular
substance from the whole body of the parenchyma. That
the entire parenchyma can thus have a secretory function
is proved by the formation by it of the fluid with which
it is permeated and its vesicles are filled and also of that
which fills the cavity of a cysticercus.

This theory seems to have originated with Leuckart
(1886, p. 367). It has been explained and defended at
great length by Looss (1893, 1894, also Braun 1893, p.
818, note) and subscribed to by Pratt (1898), Cerfontaine
(1899) and Young (1908). It is in certain respects an
unusual theory, inasmuch as it implies the absence of an
integumental covering of ectodermic origin, which is
characteristic of the rest of the Metazoa. But the life
conditions of trematodes and cestodes are peculiar and
unusual. These worms are exclusively parasitic ani-
mals, being the only large groups of Metazoa, so far as I
recall, of which this is the case, and this parasitic habit
is undoubtedly correlated with the disappearance of the
larval ectoderm and the formation of the parenchymatous
cuticula, as well as other special features of the structure
of these worms.

The most primitive trematodes, the Temnocephalidæ,
are an exception to the rest of the group in possessing an
integument composed of a cuticula with an underlying
hypodermis, although having the typical trematode struc-
ture in other respects. These animals are found adhering

to the surface of turtles and fresh-water crustaceans and are not true parasites, inasmuch as they feed upon small animals in the water and not upon the vital juices of the host. They probably form a connecting link between turbellarians and trematodes, representing the first step of the ancestors of the latter towards the acquisition of parasitic habits. The next step was taken as the result of the migration of the worms from the surface into the mouth and cloaca and on to the gills, and then into the internal organs, of the aquatic hosts. The worms thus became true parasites. They learned to feed upon the blood or the other juices of the host and were habitually enclosed or immersed in its tissues and exposed to the disintegrating action of its fluids. It is probable, as a result of these things, that the changes occurred which characterize the body-covering of these worms. The integument which is common to most worms apparently would not furnish a sufficient protection to animals thus situated, and it consequently came about in the course of their evolution that the outer epithelium with its cuticula was moulted or at least disappeared and the parenchyma acquired the property of forming a thick cuticula-like membrane on its outer surface to protect the animals from the peculiar dangers of their environment. A protective function similar to this is, as Leuckart points out, very frequently exercised by cuticula-like connective tissue structures of various kinds throughout the animal kingdom.

Von Graff (1903) has made the observation, it is interesting to note, that in certain of the parasitic turbellarians (Syncœlidium) a process similar to this has evidently gone on, for the animals have lost their integumental epithelium together with its cilia and are covered with a cuticula similar to that of trematodes.

The first steps in the formation of the cuticula have been minutely observed, as already stated, in the trematodes by Looss (1892, 1903) and Roewer (1906) and in cestodes by Young (1908). According to Looss, it first

appears as a fine line between the muscle-layers and the
outer epithelium (ectoderm) of the redia and cercaria,
which gradually broadens and when the epithelium is
finally shed, becomes the outer covering of the body.
Looss has observed this proceeding in a dozen or more
different species of trematodes and believes it to be gen-
eral to the entire group.

According to Young, the cuticula of the young cysti-
cercus is a delicate layer which is composed of a ground-
work formed of fibrillar projections of the embryonic
parenchyma cells and a homogeneous translucent cement-
like substance produced by these cells (Figs. 8 and 11).
The subcuticular cells have not yet differentiated from
the embryonic parenchyma. The young cuticula soon be-
gin to scale off on the outer surface and is constantly
being added to on the inner. In the course of time two
layers show themselves in the cuticula, the inner of which
alone contains the cement-like substance, the outer layer,
which in later stages may be very thin or be entirely lost,
forming the so-called hair-layer which sometimes char-
acterizes the outer surface of cestodes and is exclusively
fibrillar.

The later history of the cuticula is a continuation of its
larval history. Although formed principally as a secre-
tion of the parenchyma, it is at all times a part of it and
will often show, even in the adult stage, a fundamentally
fibrillar structure. It is also, as has been stated, never
moulted and can not be easily separated from the struc-
tures beneath.

Very important in a study of the whole question, is the
relation of the gonoducts and the excretory vesicle to the
surrounding parenchyma, inasmuch as the walls of these
structures have essentially the same structure as the
outer body-wall, being lined by a cuticula at the back of
which are the parenchyma and usually muscle fibers.
What then is the developmental history of these ducts?
It has recently been shown by Balss (1908) in cestodes
and Roewer (1906) in trematodes that the history of the

formation of the gonoducts as well as their structure, is essentially similar to that of the body-wall. The walls of each of these ducts (except those of the uterus in cestodes) are formed at first of a single-layered epithelium which develops from a primitive chord of epithelial cells by the appearance in it of a lumen. This epithelium, however, quickly degenerates and disappears and at the same time the surrounding parenchyma secretes a cuticula which forms the permanent coating of the tubes. The spines which are often present in the cirrus and vagina are formed in the same way.

The terminal excretory vesicle has also primitively an epithelial wall like that of the gonoducts, as has been shown by Looss (1894) and in my study of Apoblema (1898), which is replaced by a parenchymatous cuticula as in the case of the gonoducts.

The cause of the change in the structure of the walls of these ducts from an epithelium to a parenchymatous cuticula is probably identical with that which has been brought about a similar change in the structure of the body-wall. Not only is the outer covering of the animal apt to be affected injuriously by the juices of the host, but the walls of the large ducts opening to the outside as well, and both have consequently undergone an identical transformation.

What then are the origin and function of the subcuticular cells? That they belong genetically to the parenchyma has been proved with the utmost conclusiveness by the embryological researches of Looss, Young, Balss and others. The conclusion, based by Blochmann and Hein upon anatomical evidence, that they form an epithelium needs, but has not yet received, embryological support; in fact, not a scintilla of embryological evidence has been produced either by them or any one else in the thirteen years which have elapsed since Blochmann's paper was published. And purely anatomical evidence in an obscure matter like this should be received with the greatest caution, especially since the extreme parasitism of these

worms has affected all their organs and tissues in so marked a degree.

The function of these cells is a much more difficult matter to determine, and two diametrically opposed classes of views have been expressed concerning it. According to one of these, they form a specialized tissue with either a secretory or an absorptive function. According to the other, they are an unspecialized embryonic tissue, which has no direct physiological relation to the other structures of the body.

If the almost unanimous decision of all the investigators who have studied trematodes and cestodes is to be accepted, the subcuticular cells are glandular or secretory in function and, as we have seen, the cuticula is the product of their secretion. Some years ago (1898) I suggested that they (as well as the single-celled glands) may secrete, not the cuticula itself, but some substance which tends to render the cuticula immune to the disintegrating effects of the body-fluids of the host in which they pass their lives. That the cuticula of endoparasitic trematodes and of cestodes does possess some special means of protecting itself and the other tissues of the worms seems certain. Looss, for instance, has taken *Distomum tereticolle* from the stomach of the pike, where the worm was pressed tightly against the stomach-wall by large masses of actively digesting food. Something in this case must have prevented the worm from being digested, too. This special means of defense is not to be looked for in the physical structure of the cuticula itself, which is usually soft and easily injured, but in some chemical substance which neutralizes the action of the juices of the host. It is possible that the subcuticular cells secrete some such substance, especially as the ectoparasitic trematodes, which are in most cases either not surrounded by the tissues of the host or are only partially so, do not, as we have seen, possess these cells.

What the reaction of these secretions would be must depend upon the nature of the fluid in which the worm is

immersed.   If it lives in the stomach of the host, for instance, the reaction would probably be alkaline and the action of the digestive juices would thus be neutralized.   In other locations the reaction would be different and might be very complex.

A small minority of investigators, however, but important and influential though small, does not believe in the glandular function of the subcuticular cells.   Rindfleisch and Leuckart (1886, p. 366) first expressed the opinion that, in cestodes at least, they are simply peculiarly formed connective tissue cells which in certain places may lose their spindle form and assume quite the form of ordinary parenchyma cells.   This is the case, for instance, as already stated, in the scolex and between the proglottids.

Looss (1893) also regards the subcuticular cells as connective tissue structures, interpreting them as embryonic and unspecialized cells which are destined to develop into parenchyma and muscle strands as the worm increases in size, and he supports his views with such a mass of detailed observations and such cogent reasoning that it is likely they would be generally adopted if the belief in the secretory nature of the subcuticular cells were not so firmly fixed in the literature of the times.

Looss shows that the interior cells of the germ-balls of the cercaria develop into the nervous system, the genital organs, the intestinal cœca and the parenchyma—all after the first appearance of the cuticula.   But all of these cells do not at once so develop.   The young worm must grow often many thousandfold before it reaches adult size, and this increase in size is made possible through the persistence in an undifferentiated condition of certain of these interior embryonic cells, which during the life and growth of the worm are constantly forming new parenchyma cells, as well as other structures.   The formed parenchyma cells do not divide.   In the cercarian tail, which is destined to have but a very short existence, all of these cellular elements become parenchyma cells and

muscle strands and no embryonic cells persist; hence no subcuticular cells are present.

Originally these indifferent cells lie around all of the growing organs, especially the genital organs, as well as near the periphery of the body. But in the course of the growth of the worm all disappear except those near the periphery, which become the subcuticular cells and may remain throughout life, giving rise to new parenchyma cells, and also to muscle strands and to flame-cells. In old digenetic trematodes, however, they may also disappear (Lander, Maclaren). Looss compares these cells to the cambium of plants, which is also an indifferent tissue which gives rise to certain specialized tissues throughout the life of the plant.

The only authors who have fully subscribed to this theory, so far as I know, are Nickerson (1894) and Stafford (1896), who support it by observations drawn from the study of Sichocotyle and Aspidogaster, respectively, although Schuberg (1894), Lander (1904), Balss (1908), Young (1908) and others have declared in favor of the parenchymatous origin of the subcuticular cells.

That so few have done so is probably due, as I have already indicated, to the fact that the belief in the glandular nature of the cells in question is so firmly fixed in the minds of helminthologists as to have axiomatic force. But it must never be forgotten, notwithstanding this circumstance, that this particular function has never been proven for these cells. No one has yet seen them produce a secretion and the supposed ducts that are seen in connection with them in some, although by no means in all species, and the possession of which is perhaps the principal proof which has been brought of their glandular nature, are not ducts at all. In contrast to them we might indeed place the single-celled glands, whose ducts are always perfectly plain and whose secretion can be seen. It must also be remembered that neither Leuckart nor Looss, each of whom, it will be generally conceded, has surpassed all contemporary investigators in his knowl-

edge of parasitic worms, has attributed a glandular function to these cells, but, as we have seen, has interpreted them in quite a different way.

Summary

1. The cuticula of trematodes and cestodes is not homologous to that of other worms and of arthropods.

2. The cuticula of trematodes and cestodes is the peripheral portion of the parenchyma, being composed mainly of secretions of it.

3. The subcuticula is not an epithelium or a hypodermis, but belongs genetically to the parenchyma.

4. The subcuticular cells are not present in the monogenetic trematodes, in most of the Aspidobothridæ and in many digenetic trematodes, or in any trematodes or cestodes during the earliest larval stages when the cuticula first forms.

5. The function of these cells is not known, and although most authors have ascribed a glandular or secretory function to them it seems likely that they form an indifferent, embryonic tissue which develops into specialized tissues as the worm increases in size.

LITERATURE

Balss, H. H.   Ueber die Entwicklung der Geschlectsgänge bei Cestoden nebst Bemerkungen zur Ectodermfrage. *Zeitschr. f. wiss. Zool.*, Bd. 91, p. 266, 1908.

Blochmann, F.   Die Epithelfrage bei Cestoden und Trematoden.   Hamburg, 1896.

Brandes, G.   Zum feineren Bau der Trematoden.   *Zeitschr. f. wiss. Zool.*, Bd. 53, p. 558, 1892.

Braun, M.   Trematodes.   Bronn's Klassen u. Ordn., Bd. 4, p. 306, 1893.

Cerfontaine, P.   Contribution à l'Étudé des Octocotylidés.   *Arch. d. Biol.*, T. 16, p. 345, 1899.

Goto, S.   Studies on the Ectoparasitic Trematodes of Japan.   *Jour. Coll. Sci. Imp. Univ. Jap.*, Vol. 8, p. 1, 1894.

Goto, S.   Notes on some Exotic Species of Ectoparasitic Trematodes.   *Jour. Coll. Sci. Imp. Univ. Jap.*, Vol. 12, p. 263, 1899.

v. Graff, L.   Die Turbellarien als Parasiten und Wirte.   Festschrift für 1902.   Graz, 1903.

Lander, C. H.   The Anatomy of Hemiurus crenatus (Rud.) Lühe, an appendiculate Trematode.   *Bull. Mus. Comp. Zool.*, Vol. 45, p. 1, 1904.

Leuckart, R. Die Parasiten des Menschen, etc. 2te Aufl. Leipzig, 1886.

Looss, A. Ueber Amphistomum subclavatum, Rud. und seine Entwicklung. Festschrift f. R. Leuckart. Leipzig, p. 147, 1892.

Looss, A. Zur Frage nach der Natur des Körperparenchyma, etc. *Verh. Sächs. Ges. Wiss. math.-phys. Cl.*, Bd. 45, p. 10, 1893.

Looss, A. Die Distomen unserer Fische und Frösche. *Bibl. Zool.*, Heft. 16, p. 1, 1894.

Maclaren, N. Ueber die Haut der Trematoden. *Zool. Anz.*, Bd. 26, p. 516, 1903.

Monticelli, F. S. Cotylogaster michaelis, etc. Leuckart's Festschrift, p. 168, 1892.

Monticelli, F. S. Studii sui Trematodi endoparassiti. *Zool. Jahrb. Anat.*, Bd. 3, Suppl., 1893.

Nickerson, W. S. On Stichocotyle nephropis, etc. *Zool. Jahrb. Anat.*, Bd. 5, p. 447, 1894.

Nickerson, W. S. Cotylogaster occidentalis, etc. *Zool. Jahrb. Anat.*, Bd. 15, p. 597, 1902.

Osborn, H. L. On the Habits and Structure of Cotylaspis insignis Leidy. *Zool. Jahrb. Anat.*, Bd. 21, p. 201, 1904.

Pratt, H. S. A Contribution to the Life-history and Anatomy of the Appendiculate Distomes. *Zool. Jahrb. Anat.*, Bd. 11, p. 351, 1898.

Roewer, C. F. Beïträge zur Histogenese von Cercariaeum helicis. *Jen. Zeitschr. f. Naturwiss.*, Bd. 41, p. 1885, 1906.

Schauinsland, H. Beiträge zur Kenntniss der Embryonalen Entwicklung der Distomeen. *Jen. Zeitschr. f. Naturwiss.*, Bd. 16, p. 465, 1883.

Schauinsland, H. Die embryonale Entwicklung der Bothriocephalen. *Jen. Zeitschr. f. Naturwiss.*, Bd. 19, 1886.

Schuberg, A. Zur Histologie der Trematoden. *Arb. a. d. Zool.-zoot. Inst. Wurz.*, Bd. 10, p. 167, 1894.

Stafford, J. Anatomical Structure of Aspidogaster conchicola. *Zool. Jahr. Anat.*, Bd. 9, 1896.

Tennent, D. H. A Study of the Life-history of Bucephalus, etc. *Quart. Jour. Micr. Sci.*, Vol. 49, p. 635, 1906.

Thomas, A. P. The Life History of the Liver-fluke. *Quart. Jour. Micr. Sci.*, Vol. 23, p. 90, 1883.

Young, R. T. The Histogenesis of Cyticercus pisiformis. *Zool. Jahrb. Anat.*, Bd. 26, p. 183, 1908.

Zeller, E. Untersuchungen über die Entwicklung und den Bau des Polystoma integerrimum. *Zeitschr. f. Wiss. Zool.*, Bd. 22, p. 1, 1872.

Zernecke, E. Untersuchungen über den feineren Bau der Cestoden. Jena, 1895.

THE AMERICAN TOAD (BUFO LENTIGINOSUS AMERICANUS, LeCONTE). II

A Study in Dynamic Biology

NEWTON MILLER

Clark University

Hibernation

Little is known about the toad during the winter. An anonymous article in *Cornhill* states that toads go down in the mud by ponds and become encysted in balls of clay. Allen is of the same opinion. More recently Gage says he thinks they go into the ground for hibernation and not under boards, stones, etc., as supposed. Toads were found under leaves in March, 1895, by Kirkland, who also states that they "do not hibernate singly, as a rule and it is not an uncommon thing to find in winter or spring a dozen or more closely packed together under a rock, board or in some other sheltered spot." Various individuals tell me that they have ploughed up toads in the fields or dug them up in gardens or flower beds in the spring. There is little doubt that in this latitude they normally pass the winter in the ground.

Toads bury themselves for the winter or often for the day in loose earth. To do this they always go down backwards. With a forward lateral movement of the hind feet the earth is pushed out and to either side and the body forced into the hole by the front legs. The loose earth falls over the head as the toad descends, thereby filling the burrow. In this way little trace is left to tell of the whereabouts of the toad.

It is probable that those found under leaves, etc., in early spring had emerged from winter quarters during a warm spell and had taken temporary refuge in such places.

Experiment No. I.

An experiment on hibernation was begun October 8. Holes twenty-eight inches deep were dug in three different localities. Into each hole was placed the four sides of a 14 x 36 x 36 inch cage made of $\frac{1}{4}$-inch-mesh wire netting. Then the holes and cages were filled to the level of the ground. Twenty toads were placed in each cage and a wire covering sewed on, thus making an enclosure without bottom, filled with soft earth and with a free space of eight inches between the ground and the top.

Cage *A* was placed on an exposed north slope of a hill beneath two pines. The slope at this point was probably 20°, therefore no water stood in or about the cage. The ground here is at least two thirds sand and gravel. Little protection was furnished by the pines, since their lowest branches were twelve to fifteen feet above the ground.

Cage *B* was located in a dry, well-sheltered place under the drooping branches of some spruces on a hill-side facing the east. So well was it protected that the sun never reached it and very little rain or snow. The ground at this point is a sandy clay.

Cage *C* was sunk under a maple tree in a place not more than four feet above the water in a near-by pond. No protection was furnished by the maple. Ashes, sand and loam in about equal parts composed the soil at this place.

The toads for this experiment were collected from the fourth to eighth of October. Each was weighed and marked by cutting off a toe. Those in *A* were put out the eighth of October and those in *B* and *C* the following day. One to several toads were found out of the earth in one or all the cages until November 26 with the exception of the twenty-ninth of October. My notes show a very slight tendency for those in cage *A* to hibernate before those of *B* and *C*.

After the twenty-sixth of November nothing was seen

of the toads until the twenty-eighth of March, when *A* was dug up, and eleven days later cage *C*. Fourteen were found in *A*, of which only three were alive. The depths at which they were found varied from one to twenty-four and a half inches. All above sixteen inches (the depth to which the ground was frozen) were dead. In *C* thirteen were found, of which nine were alive. There had been a trench dug near one end of the cage in the fall and the earth in this end was frozen to a depth of twelve inches. Two toads near the surface and two in the frozen end, one at a depth of twelve inches, were dead. Those alive were down below the frost line, which in this place was between eight and nine inches.

The accompanying table shows the weight of each live toad at the time it was put out and when dug up, also the depth at which it was found.

CAGE C

No. of Each Toad.	Weight, October 9.	Weight, April 4.	Depth in Inches.
1	50.5	44.0	15
3	19.5	15.0	9½
4	24.0	18.8	12½
5	27.0	25.6	14½
7	32.5	26.6	20
8	27.0	23.9	10
10	24.5	21.2	16½
12	5.5	4.6	11
19	19.5	15.8	15

CAGE A

No. of Each Toad.	Weight, October 9.	Weight, March 29.	Depth in Inches.
10	16.5	12.9	17½
13	9.5	7.0	17½
19	20.5	15.0	24½

Average loss of weight 3.8 grams.
The total loss of weight was 15.3 per cent. of total weight.

B was not disturbed, and the first toad to appear was no. 1 on the thirtieth of April, and the second and last was no. 7 on the twenty-eighth of May.

Experiment II

Another experiment was made on two toads which were placed in a 7 x 7 x 7 inch wooden box that contained some four inches of rather dry clay. A stone was laid on top and the box sunk ten inches in the side of a bank composed of clay and gravel. On the first of March, when the box was dug up, the ground all about it was frozen so hard that it had to be dug out with a pick. The earth in the box had been moist enough to freeze into clods, which were easily broken with the fingers. Both toads were alive, but no. 2 died two days later without showing any other signs of life than the beating of its heart. No. 1 moved her legs feebly as soon as broken out of the clay, had her eyes open in less than five minutes and within ten minutes more she was crawling about on the snow. Only the tips of some of her toes seemed to be frozen, but these never became sore. No. 2, as far as I could detect, was not frozen more than no. 1. No. 1 began feeding on the second day and during the remainder of the winter showed no signs of hibernating.

Experiment No. III

For this experiment a 12 x 12 x 24 inch glass aquarium was used in which was placed about three inches of moist earth. Six toads properly labeled were put in the cage, which was kept within eight inches of my radiator. As I was in my room most of the day and slept there at night I could watch them closely. I had a supply of meal worms, and every time a toad appeared it was given all it would eat. They came up usually about 8:30 P.M. and buried themselves by 10:00 P.M. Frequently they shed their skins and went down at once. No. 4 had the habit of only half burying herself and, probably, one fourth of the time was spent thus, but during this time she was rarely found sleeping.

The weight and sex of each toad was as follows:

```
No. 1, ♀ ............................   8.8 grams.
No. 2, ♀ ............................  27.8 grams.
No. 3, ♂ ............................  22.2 grams.
No. 4, ♀ ............................  76.5 grams.
No. 5, ♀ ............................   6.5 grams.
No. 6,[7] ♂ ..........................  39.0 grams.
```

These toads were under daily observation from October 23 to April 1, excepting five days from December 26 to 30.   Fig. 7 is given as an average month's record
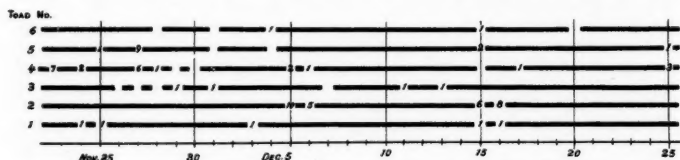
Fig. 7.   Record of six toads for one month.

of this experiment.   The continuous lines represent the time the toads spent under the earth; the breaks, the number of times the toads came up out of the earth; the figures in the breaks, the number of meal worms eaten at such times.

Experiment No. IV

This experiment was also carried on in my room, from the twenty-third of October until the eighth of April. During this time a female, weighing forty-eight grams, was kept in a small bell jar which contained, besides the toad, only a small thin piece of sponge.   The sponge was kept moist and a piece of glass over the top of the jar prevented too rapid evaporation.

When the toad was placed in the jar she was cold, numb and to all appearances hibernating, but five hours after being brought into a warm room she was wide awake, and from then on to the end of the experiment was never seen with her eyes closed nor showing the least signs of hibernation.   She fed throughout the winter, eating in all, the small number of 173 meal worms or their equiva-

[7] At the end of the experiment nos. 2, 5, 6 had increased their weight, respectively 7.4, 4 and 0.49 grams.

lent, but at no time did she go longer than nine days without feeding. Eight worms were the most she ever ate at one time, while one to three constituted her usual meal. She refused food during the day and fed only from 7 to 10 P.M.

Experiment No. V

This experiment is a duplicate of no. IV. with the exception that two small toads (about 8 grams) were used. The experiment began on the twenty-third of October and continued until the death of the toads, which, for the male, occurred December 15 and for the female, February 10. The female fed throughout this time with the exception of two periods, November 7–17 and December 18–February 10. During these two intervals she at times appeared to be hibernating or simply sleeping. It was almost a month before the male began feeding, but afterwards fed until he died. At no period did he show any tendency to hibernate. The male escaped from the cage and was found dried up. The female refused food from December 18 to February 10, became emaciated and died as though starved.

Conclusions

From experiment no. I, it is seen that toads go down into the ground to hibernate and that all of those not below the frost line in unsheltered places, perish.

Experiment no. II shows that toads in protected places can resist freezing temperature.

It is a question whether toads make any preparation at all for the winter more than simply burying deeper than they are accustomed to do in the summer. Experiment no. I shows that some had not hibernated as late as November 26. Toads are active until it becomes too cold for them to capture insects; as a cold wave comes, the toads for the first time begin to prepare for winter by digging a little deeper. As the ground gets colder,

they go further down, keeping a little below the frost line.   I have found no evidence that toads select places in the fall and then proceed to bury themselves at once to a depth of eighteen to twenty-four inches.

Toads kept in a warm room do not have periods of torpidity.   Boulenger says that batrachians never go into complete lethargy.   The one in experiment no. IV was never asleep and those in experiment no. III were always wide awake and active when dug up.   None of them became sluggish.   The female of experiment V was, at times, during two periods seen with her eyes closed, but at these times she was easily awakened by a slight touch or a jar of the cage.   At no time did she appear to be more than napping.   All of the toads kept in my room fed throughout the winter, although eating only a small quantity.   The period of least activity was from January 19 to February 19, when only one fed. Three of these toads fed eagerly during April, May and June.

There is no evidence that toads seal up their eyes, mouth and nostrils as a preparation for hibernation. Winter to the toad is only a long day, a suspension of work, a sleep.   He is ready to begin his daily routine as soon as warmed up even in midwinter.

Enemies of the Toad

When we consider the number of eggs laid and find that the number of toads does not increase, we are led to ask the question, What are the forces that keep the species in check?   If we take the low figure of eight thousand eggs for an average spawn, then all of these— as well as all the eggs of the other spawns of a single female—or the toads that develop from them, except two, must meet a premature death in order that the species may just hold its own.   This seems to be what is taking place with the toad.

What happens to this multiple of eight thousand eggs is partially known.   There is no period from the laying

of the egg until death by old age that the egg, larva or
toad is not subject to attack. I have found little evidence
of the eggs being eaten in the ponds. Crayfish confined
in the laboratory ate a few. Saprolegnnia destroy a small
per cent. of the eggs, not by attacking the fertile ones
directly, but by spreading from those that are decaying.
The gelatinous sheath which envelops the delicate eggs
is almost a perfect protection, but, as soon as the tadpoles
wriggle out of it, they are preyed upon by fish, newts,
crayfish, insects, and especially the predaceous aquatic
larvæ of insects.

I give the results of my feeding tests to show how de-
structive some of the enemies of the tadpoles are.

Species.	No.	Time.	No. Killed.	Rate per Day.
1. Dragonfly nymph, Libellula sp.?	4	May 24–June 24.	500	4
2. Dragonfly nymph, sp.?	1	June 21–June 28.	37	4.5
3. Water beetle, Acilius sp.?	1	June 21–June 30.	40	4
4. Giant w. beetle, Dytiscus sp.?	4	May 9–June 23.	4,800	26.6
5. Water tiger, Dytiscus larva.	1	June 13–June 33.	425	42.5
6. Giant w. bug, *Belostome americanum.*	1	May 24–June 26.	360	11.2
7. Newts, *Diemictylus viridensens.*	4	May 8–June 19.	1,485	9
8. Crayfish, *Cambarus bartoni.*	1	June 1–June 24.	200	8.6
9. Leopard frog larva, *Rana pipiens.*	1	July 9–July 14.	66	8.8
10. Pickerel, Esox sp.? (four inches long).	1	June 22–June 24.	80	26.6

The above tests, with the exception of nos. 2 and 9,
were made with tadpoles which were hatched from eggs
laid about April 28. Since the transformation of the
larvæ of this early laying began the twenty-second of
June, it is seen that a portion of these tests were made
with tadpoles almost ready to abandon the water. Those
for no. 9 hatched on the twenty-fifth of June. No. 2
was fed for the first five days on tadpoles of the early
spawn and the rest of the time on those hatched June
25. Only one tadpole a day was destroyed by this nymph
during the first five days.

In treating the above data it must be taken into con-
sideration that these tests were made in the laboratory
and that tadpoles constituted the whole of the food of
these animals during the tests. This is a very abnormal
condition compared with that found in nature.

Two toads just metamorphosed were found in the stomach of a green frog about a week old. Mr. E. H. Eaton tells me of finding a toad an inch long in the stomach of a leopard frog. Adult toads could not be induced to eat the young. They would take them up, but immediately reject them.

The drying up of ponds during May and June kills great numbers of the tadpoles. More than 90 per cent. of the spawn is laid in the early spring when the ponds are full. The tadpoles migrate to the shallower water, where they find food and warmth. Here they crowd into small pockets, and as the water lowers are left in the isolated puddles to perish, unless timely rains refill the pond. The "drying-up process" is disastrous not only to the larvæ, but also to the toads. Great numbers just emerged are no doubt dried up before they find damp sheltered retreats. Adults also soon perish if deprived of moist places. I give the following to show the rapidity with which transpiration and absorption of water may take place in toads. A toad weighing 4.4 grams when placed in water, weighed 5.5 grams fifty-five minutes later. One hour later, after having been kept at a temperature of 85° F. in a box made of blotting paper, it weighed 4.8 grams. Another toad treated as above weighed 3.8, 4.5 and 3.8 grams, respectively. A third weighed 39.8 grams when placed in one fourth inch of water and 49.9 grams three hours later. This is a gain of 25 per cent of her first weight. This toad was capable of reducing her weight 8.7 grams by ejecting water. From these experiments it is seen how important moisture is to the toad and why toads seek damp places.

Birds play no small rôle in the destruction of the toad. Of the domestic varieties ducks, chickens and guinea fowls are always mentioned and to these Kirkland adds geese as feeding on toads, especially the young just as they are emerging.

"Crows, grackles and several species of ducks and herons," writes A. K. Fisher, of the Biological Survey, "are known to feed on small frogs and tadpoles, and undoubtedly do not discriminate in favor of toads." He presents further evidence to prove that the screech owl must be considered as a destroyer of toads. By stomach examinations of a number of crows, W. B. Burrows finds that the toad is a common article of food. Young partridges were tested on this point. They eagerly picked up the little toads, thereby killing them, but usually refused to eat them. Miss M. Morse reports the quail as feeding on young toads. As for predatory birds, the toad is an agreeable morsel of food. Mr. Fisher writes me that he has observed the broad-winged hawk feeding on toads while the latter were spawning. He also found " five stomachs of the red-tailed hawk, eight of the red-shouldered hawk, and five of the broad-winged hawk which contained the remains of toads." From the observations of Mr. F. H. Mosher, he states that "the marsh hawk is one of the worst enemies of the toad, destroying large numbers of them during the spawning season." He also states on the same authority that a toad was found in the nest of a Cooper's hawk.

Skunks and raccoons are the only mammals reported as feeding upon toads. Mr. E. H. Short writes that in his locality skunks destroy great numbers in the late fall, and that he found in October, 1904, the remains of seven toads which had been killed in one night (by a skunk?). His evidence on this point does not seem conclusive. Concerning raccoons, Dr. H. B. Davis occasionally feeds toads to those he has in confinement.

Professor Surface records twenty-seven species and varieties of serpents from Pennsylvania, of which ten feed on toads, and two others are suspected. The feeding habits of some of these have not yet been determined and it may be found that part of them use the toad as food. Toads constitute $41\frac{1}{2}$, 20, 16 and 15 per cent. of the food, respectively, of the spreading adder

(*H. platirhinas*), the striped water snake (*R. leberis*), the common garter snake (*T. sirtalis*), and the spotted water snake (*N. sipedon*). The common garter snake and the spotted water snake are reported also as feeding on tadpoles.

Some of the game fish feed upon frogs and, presumably, they take toads also. Perhaps many toads are thus destroyed during the spawning season. We have reason to think that fishes feeding on insects and small fish devour tadpoles also. In pond no. 4 eggs were laid by the thousands and a large per cent. of them hatched, but not a single toad emerged. By the twenty-fourth of May not more than 200 tadpoles of the first laying remained and a few days later not one was to be found. There are fishes and crayfishes in this pond and the probabilities are that they destroyed the tadpoles.

Boys are very destructive to toads in the spawning season. This spring no less than one hundred and ten toads were killed about ponds nos. 1, 3 and 4. In 1897 Dr. Hodge records as one day's count two hundred dead about pond no. 4, and also that two boys had killed and carried away 300 from the same pond the day before.

Judging from my experiments, many toads die during the winter. As stated in the chapter on hibernation, sixty toads varying in size from 2 to 55 grams were put out in cages in the fall. Neglecting those under five grams (which I have reason to think escaped before cold weather) there were left fifty-one, of which only fourteen came out alive in the spring. This is a loss of 72.5 per cent., which surely must be above normal. However, further experiments and observations lead me to think that toads are killed if completely frozen. January 30, I permitted a toad 6.5 cm. long to bury itself in a cage containing a mixture of moist clay and loam. The cage was then subjected to a temperature of $-10°$ F. for twenty-four hours. At the end of this time the toad was frozen solid, and when thawed out showed no signs of life.

Another experiment, begun December 28, temperature 54° F., was made on five toads ranging between 3 and 7.5 cm. in length.   These toads were put in a wire cage filled with leaves and then buried in leaves, which had drifted into an angle of a building.   March 13, the cage was examined and all the toads found dead.   These toads during this time had been subjected to several days of 0° F., weather.

On March 28 I examined a drift of leaves.   Two dead toads were discovered half buried in the ground beneath leaves.   There were about eight inches of leaves over them.

Contrary to these observations are those Kirkland, which might lead one to infer that toads can pass the winter successfully under leaves in this region.   But as Mr. Kirkland's observations were made in March, and as toads in favorable springs emerge from their winter quarters in this month, we are inclined to believe that those he found under leaves had previously come out of hibernation and had taken temporary refuge where he found them.

The sewers of a town constitute a most destructive trap for toads.   Sewer cleaners tell me that they take out "piles of toads" especially in the fall and spring.   Examination of the "man holes" in May shows that there are on an average four toads in each one.   At this rate, for Worcester alone, there are no less than 24,000 toads thus caught, which probably means their death also.   It is making a low estimate to say that 50,000 toads perish annually in the sewers of Worcester.   It is very probable that more adult toads in a city are killed by this means, alone, than by all others combined.

I give the following table as a rough estimate of the part that each known factor plays in holding the species in check.

Percentage of destruction until time of metamorphosis caused by:

Non-fertile eggs .... 15 per cent.
Drying up of ponds .... 25 per cent.
Insects, newts, fish, etc. .... 39 per cent.
Fungi .... 1 per cent.
Disease .... 5 per cent.
   Total .... 85 per cent.

The remaining 15 per cent. may meet the following fate:

Drying up .... 20 per cent. = 3 per 100 eggs.
Domestic fowls and other birds ... 10 per cent. = 1.5 per 100 eggs.
Reptiles .... 6 per cent. = .9 per 100 eggs.
Boys .... 2 per cent. = .3 per 100 eggs.
Sewers, wells, etc. .... 15 per cent. = 2.25 per 100 eggs.
Mechanical means .... 10 per cent. = 1.5 per 100 eggs.
Winter .... 25 per cent. = 3.75 per 100 eggs.
Disease .... 3 per cent. = .45 per 100 eggs.
Miscellaneous (*including old age*) .. 9 per cent. = 1.25 per 100 eggs.
  Total .... 100 per cent. = 15 per 100 eggs.

SUMMARY

B. l. americanus spawns from the latter part of April to the first of July.

This species lays in small ponds and only a portion of each is used as a spawning ground.

The males are the first to reach the water in the spring.

88.8 per cent. of all the toads in a pond at any given time are males. Males are in proportion to females as 80.7 : 100.

Trilling in the full vigorous voice is heard only during the mating season.

Females respond to the call of the males.

Males will not hold other males.

Spawn may be deposited at a depth of eighteen inches or more. This depth does not affect materially the hatching.

Fertilization takes place in an improvised basket formed by the hind feet of the male and the body and hind legs of the female.

85 per cent. of the eggs laid in natural ponds are fertile.

Oviposition requires six to eighteen hours.

The laying of two or four strands of eggs at a time can not be considered of specific importance.

Toads lay 3,900 to 15,800 eggs at one laying.

The eggs hatch in two to six days, depending upon the temperature.

Metamorphosis takes place in thirty-two to two hundred days.

On an average the tadpoles double their weight seven times in thirty-two days.

The tadpoles are omnivorous.

Toads feed entirely on animal matter. No food is taken unless it shows signs of life.

Toads refuse no insects, worms or slugs which they can swallow.

On an average toads feed only once in a day and a half.

The average amount eaten in a day by a toad is 1.12 grams.

About 80 per cent. of the toad's food consists of harmful insects.

Toads may be active from the latter part of March to the middle of November.

Toads are chiefly nocturnal.

Toads go into the ground to pass the winter.

The greater per cent. of those that do not get below the frost-line perish.

In the strictest sense of the term, toads do not hibernate if kept in a warm place.

Toads feed throughout the winter if kept warm, although eating comparatively little.

No preparation is made for the winter other than burying to a depth below the frost line.

Some toads do not hibernate until after the middle of November.

The eggs are seldom eaten by other animals.

Great numbers of tadpoles are destroyed by insects and insect larvæ.

Birds, fishes and reptiles feed upon tadpoles.

A large per cent. of the eggs and larvæ are killed by the lowering of the water.

Toads are destroyed, chiefly, by all classes of verte-

brates; by drouth and winter, and by the sewer systems
of towns.

LITERATURE

1876. American Encyclopedia, Vol. XV, pp. 777–9.

1899. Allen, G. M. Notes on the Reptiles and Batrachians of Intervale, New Hampshire. *Proc. Bost. Soc. Nat. Hist.*, Vol. XXIX, pp. 63–75.

1865. Allen, J. A. Catalogue of the Reptiles and Batrachians of Massachusetts. *Proc. Bost. Soc. Nat. Hist.*, Vol. XII.

1895. Assheton, R. Notes on the Ciliation of Ectoderm of Amphibian Embryo. Vol. XXXVIII, p. 465.

1892. Beddard, F. E. Animal Coloration. London, p. 159.

1894. Bos, J. R. Amphibia, Agriculture, Zoology, pp. 79–81.

1897. Boulenger, G. A. The Tailless Batrachians of Europe, Vol. I, pp. 23–67; Vol. II, pp. 221 ff.

1892. Boulenger, G. A. Poisonous Secretions of Batrachians. *Nat. Sci.*, Vol. I, pp. 185–190.

1896. Brimley, C. S. Batrachians found at Raleigh, North Carolina. AMER. NAT., Vol. XXX, p. 500.

1886. Brocchii, P. Crapud. Traité de Zoologie Agricole, pp. 240–242.

1833. Buckland, W. On the Vitality of Toads Enclosed in Stone and Wood. *Amer. Jour. Sci.*, Vol. XXIII, pp. 272–277.

1901. Conradi, A. F. Toads Killed by Squash Bugs. *Science*, Vol. XIV, p. 816.

1884. Cope, E. D. Batrachians of the Permian Period of North America. AMER. NAT., Vol. XVIII, pp. 26–29.

1896. Cope, E. D. The Geographical Distribution of Batrachians and Reptiles in North America. AMER. NAT., XXX, pp. 886–902 and 1003–1026.

1889. Cope, E. D. Batrachians of North America. Bull. U. S. Nat. Mus., No. XXXIV, pp. 277–281.

1907. Courtis, D. A. Response of Toads to Sound Stimuli. AMER. NAT., Vol. XLI, pp. 677–682.

1886. de Fischer, J. Rôle des Amphibians en Agriculture.

1906. Dickerson, M. C. Bufo lentiginosus americanus. The Frog Book, pp. 63–88.

1905. Ditmars, R. L. Batrachians of the Vicinity of New York City. *Amer. Mus. Jour.*, Vol. IV, pp. 186–190.

1898. Gage, S. H. The Life History of the Toad. College of Agriculture, Cornell University.

1898. Gage, S. H. Hibernation, Transformation and Growth of the Common Toad (*B. l. americanus*). *Proc. Amer. Ass. Adv. Sci.*, XLVII, pp. 374–375.

1901. Garman, H. The Food of the Toad. Ky. Agri. Exper. Station Bull., No. 91, pp. 62–68.

1902. Garman, H. Synopsis of the Reptiles and Amphibians of Illinois. Bull. Ill. State Lab. Nat. Hist., III, pp. 335–339.

1906. Hartman, F. A. Food Habits of Kansas Lizards and Batrachians. *Tr. Kansas Acad. Sci.*, XX, pt. 2.

1903. Hay, W. P. On Batrachians and Reptiles. *Forest and Stream*, LX, pp. 425–6.

1882. Hinckley, M. H. Mouth Structures of Tadpoles of Anurous Batrachian. *Proc. Bost. Soc. Nat. Hist.*, XXI, pp. 307–314.

1898. Hodge, C. F. The Common Toad. *Nature Study Leaflet*, Worcester, Mass.

1875. Huxley, T. H. Amphibia. Encyclopedia Britannica, 9th ed., I, pp. 750–771.

1907. Kellicott, W. E. Correlation and Variation in *B. l. americanus. Jour. Exper. Zool.*, IV, No. 4.

1901. King, H. D. The Maturation and Fertilization of the Egg of *B. lentiginosus. Jour. Morph.*, XVII, pp. 293–330.

1907. King, H. D. Food as a Factor in the Determination of Sex in Amphibians. *Bio. Bull. of Marine Bio. Lab.*, XIII, No. 1, pp. 40–56.

1904. Kirkland, A. H. The Habits, Food and Economic Value of the American Toad. Mass. Agri. College Bull., No. 40.

1882. Legrips, M. V. Vitality of Toads. *Knowledge*, I, p. 202. (This is probably Buckland's experiment and misquoted, as the same experiments are given with the same result. See "Cosmos.")

1904. Morse, M. Batrachians and Reptiles of Ohio. Bull. Ohio State Univ., Series 8, No. 18, pp. 96–123.

1871. Putnam, F. W. Some Statements concerning the Frogs and Toads found at Cambridge, Mass. *Proc. Bost. Soc. Nat. Hist.*, IX, pp. 229–230.

1888. Ryder, J. A.. "Ventral Suckers" or Sucking "Disks" of Tadpoles of different Genera of Frogs and Toads. AMER. NAT., XXII, p. 263.

1901. Sharp, D. L. Wild Life near Home, p. 313.

1905. Short, E. H. Editorials (on Skunks). *Oologist*, XXII, pp. 132–135. and 188–190.

1900. Slonaker, J. R. Some Observations on the Daily Habits of the Toad (*B. lentiginosus*). *Ind. Acad. Sci.*, pp. 167–170.

1906. Stone, W. Amphibians and Reptiles of New Jersey, Pennsylvania and Delaware. AMER. NAT., XL, pp. 159–170.

1863. Verrill, A. E. Catalogue of Reptiles and Batrachians found in the Vicinity of Norway, Maine. *Proc. Bost. Soc. Nat. Hist.*, IX, pp. 195–199.

1882. Yarrow, H. C. North American Reptiles and Batrachians. Bull. 24, U. S. Nat. Mus., pp. 166–167.

OBSERVATIONS ON COPULATION AMONG CRAWFISHES WITH SPECIAL REFERENCE TO SEX RECOGNITION

DR. A. S. PEARSE

UNIVERSITY OF MICHIGAN*

DURING the past winter the writer kept about three hundred crawfishes in aquaria for a couple of months and had opportunity to observe their copulating reactions from time to time. As the published statements in regard to sex recognition in the genus Cambarus are somewhat meager, the results of some of these observations may be of interest. The species represented in the aquaria were, *Cambarus blandingi acutus* Girard, *C. diogenes* Girard and *C. virilis* Hagen. Most of the observations here recorded were made upon the last-named species, but nothing was observed in the behavior of the others to make it appear that there was any essential difference in the mating reactions of these forms.

Andrews[1] was the first to give a careful account of copulation in the genus Cambarus. He discovered that while the male holds the female on her back beneath him a spermatophore is transferred from his abdominal appendages to the cavity within the annulus ventralis of the female, where it remains sealed up until the eggs are laid. Andrews gives an excellent account of the details of the process but refers only indirectly to sex recognition. He remarks (p. 868):

When a male is put into a vessel with a female he seems ere long to become aware of the presence of the female and does not act as he does when only males are present. The female generally retreats and may

even resist the attacks of the male, but generally this is not done with much vigor, and very soon after being seized by the male the female passes into a state of passivity, resembling death.

Hay[2] in a recent paper makes statements which give a somewhat different aspect to the matter. In speaking of an hermaphrodite crawfish he says (p. 228):

It might be added that during the time the specimen was kept alive it was seen in conjugation with a female of the same species and a little later was itself seized and held for a short time in the usual manner by a male. The latter, however, is a matter of little importance, as I have several times observed the same thing in the case of two males neither of which was hermaphrodite.

An adult male of the genus Cambarus is easily distinguished from a female of the same species by his larger chelæ and narrower abdomen, and the sex of any individual can of course be accurately determined by examining the first two pairs of abdominal appendages. Whether such differences are as readily discriminated by the sensory receptors of a crawfish as they are by the human eye is perhaps open to question. According to the quotation from Andrews it would appear that a male is able to recognize a female as such, but the statements of Hay might be interpreted in such a way as to lead to the opposite conclusion.

A series of five experiments was carried out to test the ability of male crawfish to discriminate members of the opposite sex. In the different experiments from two to seven males were separated from females which they had been holding and put together in a flat circular dish (which measured thirty centimeters in diameter and contained clean water to a depth of about five centimeters). After such treatment the crawfishes were active for a time and moved restlessly about the dish. During this period of activity one male often tried persistently to copulate with another male, but such attempts were always resisted, and, although individuals were turned

[2] Hay, W. P., " Instances of Hermaphroditism in Crayfishes," Smithonian Misc. Coll., Vol. 48, 1905, Pt. 2, No. 1593, pp. 222–228.

over in some cases, they always eventually succeeded in freeing themselves. After these males had been allowed to " fight " thus among themselves for from half an hour to two hours (the time varied in different experiments) they became comparatively quiet and finally came to rest in a group at one side of the dish in such a way that their bodies were in contact with each other. After they had remained in this condition of rest for at least half an hour a female which had just been released from copula-tion with a different male was gently introduced into the dish with them.

In all five of the experiments the female moved about the dish and came in contact with one or more of the males, and sometimes she even walked over them, but nevertheless there were only two attempts at copulation within half an hour after a female had been placed in the dish. In one of these cases a male attempted to grasp another male after the female had been introduced, but he soon desisted from the attempt and all the individuals in the dish then became quiet again. In the other instance one of the (two) males attempted to turn over the female as soon as she came in contact with him (not as soon as she was introduced into the dish). These experiments showed that males which had recently been in active copu-lation were not necessarily induced to copulate again by the immediate presence of an active female.

Five other experiments were performed which were similar to those just described except for the fact that the female was introduced into the dish with the males before they had come to rest. In this second series copu-lation took place within half an hour in every case. The results make it appear that the readiness with which copu-lation is undertaken by a pair of crawfishes depends upon the physiological state of the male, for, as Andrews has stated, the male usually takes the active part in the ma-ting reactions, while the female remains passive.

Another series of observations showed that the readi-ness with which copulation takes place depends largely

upon the " chance " coming in contact of two individuals
which are in proper physiological state. On five differ-
ent occasions when the aquarium, which contained two
hundred crawfishes, was visited and no pairs were found
to be copulating or attempting to do so, all the individuals
were dragged into the center of the aquarium and heaped
together in a pile. They were then allowed to remain
undisturbed for half an hour. During this time there was
an active scramble and many individuals necessarily came
in contact with each other. In all the experiments from
three to five pairs were found to be in copulation at the
end of the half hour. These observations showed that
individuals had been present in the aquarium which were
in the proper physiological state for copulation, for as
soon as they came in contact with each other the usual
mating reaction took place.

There are many factors which might possibly exert an
influence on the copulatory reflexes of a crawfish and it
is easily conceivable that such stimuli as temperature,
light and chemical substances might be of importance in
this connection. In regard to temperature Bell[3] has ob-
served (p. 625) that, after a number of individuals had
been warmed,

The males showed marked sexual activity, rushing up to the females,
pushing them about, seizing them and trying to turn them over in spite
of their vigorous resistance. One of the males did succeed in turning
a female on her back twice, although she struggled violently to escape—
a thing which a female never does in the ordinary sexual act.

He concluded that, " the rise of temperature seemed to
stimulate the males to sexual activity but not the fe-
males." During the present experiments it was observed
that there were fewer cases of copulation when the tem-
perature of the water in the general aquarium was below
11° C. than when the temperature was above that point.
Apparently temperature is of some importance as exert-
ing an inhibitory or excitatory action on the copulatory
impulse.

[3] Bell, J. C., " Reactions of the Crayfish," Harvard Psychol. Ser., Vol.
2, 1906, pp. 615–644.

Chidester[1] has recently shown that the general activity
of crawfishes is greater at night and it would therefore
seem probable that copulation would be more likely to
take place in the dark than in the light. In order to ascer-
tain if this supposition was correct, two oblong dishes
were placed side by side in front of a window and were
filled to a depth of five centimeters with water which was
of the same temperature in the two dishes (11° to 14° C.
in different experiments). One of the dishes was allowed
to remain exposed to strong light, but not to the direct
rays of the sun, and the other was completely enclosed in
a tight wooden box which was painted black on the inside
and covered by a movable lid. In each experiment two
pairs of crawfishes which had been copulating or attempt-
ing to do so were isolated and a separate male and female
placed together in each dish, after which their behavior
was noted at short intervals of time. In order to elimi-
nate the effects due to the individuality of any particular
crawfish, the individuals of each quartette were changed
about as much as possible in successive trials. After the
first copulation, the male was changed from the dark dish
to the one in the light, and the male which had been in the
light took his place; after the next trial the pairs were
interchanged, and finally the two females were changed
about. By this method of procedure there was an oppor-
tunity to compare the rapidity of copulation in the light
and in the dark. The results of the experiments are
given in Table I.

TABLE I.

Showing the results of seven experiments to ascertain whether certain
crawfishes would copulate more quickly in dark or in light. (L indicates
that the pair in the light copulated first; D, the pair in dark copulated
first; E, both pairs copulated at the same time.)

Experiment.		1	2	3	4	5	6	7
Trial 1		L	D	L	L	L	D	D
Trial 2	♂ ♂ interchanged	D	E	D	L	L	L	D
Trial 3	Pairs interchanged	L	L	D	D	D	D	D
Trial 4	♀ ♀ interchanged	L	E	L	D	L	D	D

[1] Chidester, F. E., " Notes on the Daily Life and Food of Cambarus
bartonius bartoni," Amer. Nat., Vol. 42, 1908, No. 503, pp. 710–716.

In twelve of the trials copulation took place first in the light; in fourteen cases the pair in the dark copulated first, and in the other two instances the two pairs occupied the same period of time in becoming united. Twenty-eight different individuals were given twenty-eight opportunities to copulate and approximately an equal number of " first " copulations took place in the light and the dark. From these experiments it appears that conditions of light stimulation are apparently of little consequence, at least where individuals which are in a state of excitement are concerned.

Attempts were made to arouse males to a state of activity by adding extracts to the surrounding medium. The males were separated from their mates and allowed to become quiet in a dish of clean water. Various portions of females which had been recently copulating were then added, and although pieces of ovary, pieces of abdomen and extracts from these organs and from the whole body were used in this way, nothing but negative results were obtained. The males remained quiet and exhibited no signs of excitement within half an hour after the portions of the female's body had been added. From these results it does not seem probable that copulation is brought about by the action of any secretion given off by the female which might serve to excite the male.

The results of all the experiments described indicate that sexual union is more or less a matter of chance. If a male and a female which are in the proper physiological condition come together they will copulate with equal readiness in the light or dark. Neither sex can be said to be wholly responsible for the act of sexual union and although the male usually assumes the active part, it is not an invariable rule. An instance was observed in which one female fought almost continuously with another for over two hours. When this pugnacious individual was placed in a dish with several males she walked about actively and grasped them with her chelæ, but as soon as one of them grasped her and attempted to turn her over,

she became quiet and was soon in copulation. If we examine Table I it will be seen that in experiments 1 and 6 the same male copulated first in four of the trials, but in experiments 2, 4 and 5 the male which copulated first in trial 1 was equalled or excelled by the rival male in the three succeeding tests. No female copulated first in all four trials.

In all the observations cited no evidence was seen which would go to show any power of sex descrimination in the crawfish. During the mating season the instinct of the male is to grasp and turn over every crawfish which comes in his way. The method is one of trial and the result of such random movements depends largely upon the reactions of the individual with which copulation is attempted. If this individual is a female of the same species the attempt may meet with success but if it is a male or a female of another species the effort at sexual union is usually of short duration. The lack of discriminative ability on the part of the males is shown by the fact that they often attempt to copulate with individuals of their own sex. This fact in itself is not of course very conclusive as similar behavior is often observed in many higher animals, such as dogs and cattle, in which the males are doubtless able to recognize the females as such. Furthermore, on two occasions males were observed to be in copulation with females which had been dead for twelve hours and in another instance a male of one species (*Cambarus virilis*) was found in copulation with a dead female of another species (*C. blandingi acutus*). This last observation is of especial interest for, as Andrews[5] says (p. 474) it is not known " whether the male stylets and the female annulus are closely adjusted to each other in each species or not. Experiments should at least decide whether the males of one species can fill the annuli of other species or not." The observation just cited shows that two different species can at least

[5] Andrews, E. A., " The Annulus Ventralis," Proc. Boston Soc. Natur. Hist., Vol. 32, 1906, No. 12, pp. 427–479, pl. 43–48.

unite sexually as I was careful to observe that the stylets of the male were actually inserted into the annulus of the female. Whether a spermatophore can be transferred under such circumstances is of course still a question.

The observations described in this paper would lead to the conclusion that the crawfishes have little or no power of sex discrimination. The male " tries " every crawfish which he meets and the instinct of the female is to remain passive under such treatment while another male will attempt to escape. The sexes come together as the result of random movements or in the course of the daily travelling about in search of food. Holmes[6] reached similar conclusions as a result of his observations on amphipods. Male amphipods, however, would not attempt to copulate with a dead female and in this respect their powers of discrimination apparently excel those of the crawfish.

[6] Holmes, S. J., " Sex Recognition among Amphipods," *Biol. Bull.*, Vol. 5, 1903, No. 5, pp. 288-292.

SHORTER ARTICLES AND CORRESPONDENCE

DEGENERATION ACCOMPANYING INBREEDING

It seems now generally conceded that inbreeding per se is not injurious but that when a similar defect in the germ plasm comes from both sides of the family the children do not rise in respect to this character above the parental level. The effect of close inbreeding in small isolated communities is, at any rate, always interesting, and affords an excuse for the following note, based on facts gleaned from a letter sent me by Rev. H. East, a missionary whose headquarters are at Haka, Chin Hills, Burmah.

Rau Vau village has been isolated for about seven generations. It contains about sixty houses and possibly two hundred inhabitants. Of these ten are idiots, many are dwarfs and some hydrocephalic. A number of cases of syndactylism and brachydactyly occur. Mr. East was not able, offhand, to state how these peculiarities are inherited, but it is to be hoped that he will be able to report on this subject later. Certainly, heredity in such a community deserves careful attention.

C. B. Davenport.

A NOTE OF THE PRAIRIE-DOG OWL WHICH RE-SEMBLES THE RATTLESNAKE'S RATTLE

In looking over an earlier number of the American Naturalist[1] I find a note under this head by F. B. Loomis in which he describes a note of the adult burrowing owl which so closely resembled the rattle of a rattlesnake that not only the members of his party, but their horses as well, were deceived.

. . . it alighted and began a third rattle; and this time all saw its stretched neck, bulging eyes, open beak and vibrating tongue. The whole appearance of the bird indicated assurance that it would thus frighten off any enemy; and it certainly deceived the four plain-bred horses, as well as the men, all of whom had for weeks been familiar with rattlesnakes, and two of them for years.

This reminds me that about sixteen years ago I made some observations on the same subject. It is particularly interesting

[1] Am. Nat., Vol. XLI, pp. 725–726, 1907.

to me to note that the horses were invariably frightened by the "rattle," for in thinking of my own experience I have often considered that perhaps my observations were somewhat prejudiced that rattlesnakes are so popularly supposed to occupy the holes with the owls. The observations which Loomis records here were for an adult bird, while mine were upon the young.

A burrow was dug out and a nest of eight young secured. When taken from the burrow, and with great frequency, these young birds—still in the downy condition—made this sound. As I remember it, this occurred every time they were disturbed. These birds were taken in Cheyenne or Rawlins County, Kansas, while Loomis's observations were made in Wyoming. Loomis seems to regard the note as peculiar to the one individual he observed, for he writes:

.If it succeeds in teaching this trick to its young, a protective habit of great value will be formed.

Whether the prairie-dog owl generally has this note I am quite unprepared to say, but my observations in northwestern Kansas indicate that it is not an individual peculiarity. It is so easy to attribute adaptive significance to characters that our attitude toward such suggestions should always be very critical; whether the note described is ever of any service to the bird would be a difficult problem for a field ornithologist. It would be interesting to know whether notes of this kind are peculiar to the prairie-dog owl, or whether they are also heard in species which have no possible association with the rattlesnake. Some one familiar with birds in the field could probably answer this question.

J. ARTHUR HARRIS.

NOTES AND LITERATURE

THE CAUSATION OF SEX[1]

THIS book is the work of a general practitioner of medicine. For twenty years he has collected clinical facts and materials upon which he now claims to have built up a new theory of sex. The theory has been put to the test in forecasting the sex of the unborn child and proved adequate in 97 per cent. of cases. The cause of sex being known in man, the determination of sex is readily accomplished. A summary disposition of Schenk's once-famous superior-vigor-theory is made by simply citing the clinical fact of the occasional simultaneous birth of both a boy and a girl.

The theory dissociates absolutely the male parent from any influence in sex causation—thus differing from several otherwise closely similar hypotheses. It is simply that "sex depends upon which ovary supplies the ovum fertilized." The clinical materials employed in proof are: (1) Sexually differing families; (2) extra-uterine pregnancy; (3) pregnancy in double uteri; (4) multiple pregnancy; (5) migration of ovum (internal and external; (6) preponderance of male over female births. Furthermore, the author denies validity to all arguments, respecting sex in man, from analogy with invertebrates or even lower vertebrates, believing "women not analogous to any living thing."

Respecting the anatomy and physiology of the female generative organs the following facts are noted and employed in the construction of the theory: (1) Lower position in pelvis of right ovary and internal opening of right oviduct; (2) larger caliber of right oviduct; (3) larger size of right ovary; (4) occasional presence of two ova in a Graafian follicle; (5) recorded cases of double nuclei in the mammalian egg; (6) corpus luteum as indicator of ovary from which the impregnated ovum came; (7) dependence on common cause, consequently close coincidence, of ovulation and menstruation (proof: scars of corpora lutea correspond to the number of menstrual periods experienced). The

[1] "The Causation of Sex," by E. Rumley Dawson, London, H. K. Lewis, 1909, pp. 190, 21 illustrations.

foregoing statements are supported mainly by quotations from various recognized authorities.

Chapters 3 and 5, dealing with the Formation of the Ova and Fertilization respectively, are vulnerable at various points to the criticisms of gratuitous assumption, specious reasoning and flagrant disregard of recent biological advance, more particularly respecting the questions of heredity and sex. Absolutely no notice is taken of the work of Bateson, Davenport and Castle on Mendelian inheritance, nor of the cytological and experimental results concerning the determination of sex respectively of Wilson and Correns. But however scant the appreciation of the bearing of results from non-human materials on the general problem, and however radical the ideas here expressed, the theory as such remains essentially unaffected.

In chapter 3 it is urged that "Each ovum has its own definite and unalterable sex, being either male or female according to the ovary from which it is derived." Though microscopic evidence of such difference is not yet forthcoming it is asserted to obtain "just as between the eggs of two different women." "Similarly the ovum of a negress is indistinguishable by our present appliances from the ovum of a blonde, yet we know full well that if fertilized one produces a black child while the other gives rise to a white one" (p. 29). Assuming, as this line of reasoning does, that there is identity (or at least close similarity) between the process of sex-inheritance and color-inheritance, both would seem to be due, in a large measure, to the influence of the male. For the ovum of a negress fertilized by the spermatozoon of a blonde male might give rise to a black child, but it would more likely be a mulatto, perhaps almost indistinguishable from a blonde—similarly sex may be influenced or determined by the spermatozoon.

Identity in the mechanism of heredity, whether it concern sex, color or other unit characters, is widely accepted; but Dr. Dawson seems to posit such identity or the absence of it depending upon the conclusion he desires to reach. Above he posits identity; but he reasons incorrectly in an attempt to reach a desired conclusion.

In a later chapter (chapter 5), starting with the assumption that the "provision in the human ovum of multiple avenues of entrance (the radiating pores of the zona pellucida) looks as though multiple spermatozoa are required to enter thereby in order to fertilize the human ovum," he argues that the "differ-

ent number of paternal and maternal features and character-
istics inherited by the respective children must be due to a vary-
ing quantity of the paternal body or germ-plasm carried to each
ovum fertilized by the varying number of spermatozoa'' (100
or more). He argues for the necessity in human fertilization of
multiple spermatozoa on the basis of (1) prolific supply at each
ejaculation (200,000,000—Lode) ; (2) very frequent renewal; (3)
long life in oviduct. According to this argument the color
of the child resulting from the development of the egg of a
blonde fertilized by the spermatozoon of a negro would be
blonde if only one sperm entered, black if many entered—the
direct contrary of his former position.

Again, the author holds that there is no question of heredity
or ''the exhibiting of ancestral tendencies or peculiarities in a
varying degree'' among the invertebrates! All that is necessary
here at fertilization is to provide stimulus to development; con-
sequently one spermatozoon will do. Even among cod or her-
ring one sperm is held to be sufficient for the same reason. The
number of spermatozoa demanded for the expression of any
particular degree of inheritance is believed to be indicated by the
number of micropyles in the egg. If always only one, or the
same number of spermatozoa, entered the human ovum there
could be no such thing as somatic variation. Evidently our
author knows little of the later studies on the nature of fertiliza-
tion and the function of the chromosomes in relation to sex and
general inheritance. It is stated that ''many spermatozoa en-
tering the ovum lead to a father-like child whether boy or girl;
a few only entering leave the yolk still maternally superior or
prepotent so that the child whether boy or girl takes after the
mother'' because it is too much to ask of a single chance sperma-
tozoon ''besides fertilizing the ovum nucleus, also . . . to settle
the sex of the coming child and likewise impart to the oosperm
the form and face, talents and tendencies, coloration of hair,
skin and eyes, movements and mannerisms, and even diseases of
the father'' (p. 42). And yet by the hypothesis that in the
chromosomes of a single spermatozoon reside such potency can
be explained the various phenomena of Mendelian inheritance
—moreover, characters can be added and subtracted in accord
with this theory. How could the phenomenon of color domi-
nance in mice and guinea-pigs be explained on Dawson's as-
sumption? Of course he will always reply that there is no

analogy between heredity in guinea-pigs and the human female. Evidently he has not yet accepted even the fact of evolution.

Absolute identity of the process of fertilization is asserted to be disproved by the results of merogony. The connection is obscure, but if the findings of Boveri and Delage in echinoderms have any bearing on the matter it would be to show that a single spermatozoon is prepotent over the greater extranuclear mass of the ovum and determines an organism with male characteristics.

Similar examples of loose reasoning and unwarranted statement appear in chapter 6. Here it is said that it is "reasonable to suppose that the association of the left ovary with the production of the female sex is due to the fact that the weaker sex should result from the weaker side of the body." How will Dr. Dawson prove that the female is the weaker sex, or that the left side of the brain is the weaker, or that left-handed persons are weaker on that side? "To inquire why the ovary of the right side should have been chosen for the production of boys rather than the other side seems as fruitless and as useless as to inquire why the liver should have been placed to the right and the spleen to the left of the body." Surely this is giving a curious turn to the method of reasoning by analogy. The position of the liver and spleen, as also of the stomach and other viscera, is determined largely by the mechanical factor of pressure under which they mutually adapt themselves to their narrow confines. Originally they also were symmetrically placed with respect to the body axis as are the gonads and kidneys which remain so definitively. With as much reason might one argue that the right eye sees only the upper colors of the spectrum and the left the lower, or that one kidney secretes the mineral and the other the organic matter of the urine or that the right testicle gives rise to blondes and the left to brunettes.

All this, however, has little bearing on the essential point of the theory, which is based upon the following facts and cases: (1) Woman has one-sexed children only by different men; (2) father produces both-sexed children with different wives but only one sex with each wife (in both of these instances the woman is supposed to be unilaterally sterile); (3) man gets both-sexed children with one of his wives but only one sex with the other "because she is unilaterally sterile." If it depended on the male, it is argued, he should get both-sexed children with both wives. The theory is further supported by animals also: (1) cow covered by fifteen bulls has seventeen calves, all female;

(2) mare covered by more than six different stallions had ten foals, all male; (3) bitch covered by two different stud dogs gave birth in two litters to six male dogs; (4) sow gave birth to a litter of ten boar pigs. In all these cases the female is supposed to have been unilaterally sterile. One might urge against the cogency of these facts as supporting the theory that the law of probability and the hypothesis of Mendelian dominance could explain them as well as the supposition of unilateral sterility.

In chapter 8 cases of pregnancy are reported to prove the theory. The proof here consists in showing cases of male and female pregnancy with the corpus luteum in the right and left ovum respectively; six cases of the former are given, and three of the latter (one doubtful). Among the vast number of possible cases, these eight might very well be mere coincidences—for when exceptions occur he invokes the aid of a migration of the ovum.

Chapter 9 considers cases of extra-uterine pregnancy to prove the theory. Twelve cases are reported of tubal pregnancy and a corpus-luteum-bearing ovary on the same side. Accordingly, if pregnancy be in the right oviduct and the fœtus a male, one is justified in declaring the ovum came from the right ovary. Nine such cases are described; and five in which a female fœtus was found in the left oviduct. Furthermore, two cases of twin-pregnancy, one extra-uterine and the other intra-uterine are shown to conform to the rule. Dr. Seligson of Moscow, is said to have collected fourteen cases of males developing in the right tube and females in the left. Two cases of right ovarian pregnancy of male sex are given, and one reverse case.

Chapter 10 takes up cases of pregnancy after unilateral ovariotomy. Five examples of male births after removal of the left ovary are submitted, and four where females were born after the right ovary was removed. A case is reported of right ovariotomy combined with resection of the left ovary, followed by the birth of a girl. Many exceptions are admitted, but they are ascribed to incomplete removal of the ovary in question, or the regeneration of ovarian tissue from the pedicle, or to the presence of an accessory ovary. Thus these examples lose much of their force.

Cases of pregnancy in abnormal uteri are discussed in chapter 11. Seven cases are recorded, four in which the right halves of double uteri were pregnant with males, and three where the left halves contained females. Exceptions, which are frequent, are

charged to a migration of the ovum from one side to the horn of
the opposite side. And ''in those animals such as pigs, cats, rab-
bits and mice—whose offspring are truly multiple—the fœtuses
are mixed up in the two cornua; but . . . . . the ovaries contain
between them a corresponding number of corpora lutea, both
individually as regards sex and collectively as regards num-
ber'' (p. 98).

An interesting presentation is given in chapter 15 of supposed
reasons why more boys are born than girls. Statistics recorded
for over 200 years show this to be a fact, the proportion being
106 males to 100 females. More boys are said to be born by rea-
son of the greater number of male eggs liberated, and by reason
of easier access of spermatozoa to male ova, both due to the
anatomical facts above enumerated. Nature thus attempts to
compensate for the greater male mortality at birth and during
the first five years.

Multiple conceptions are brought under the hypothesis. The
woman is held responsible for plural pregnancies; nevertheless
the author is forced to admit exceptional cases (p. 144).

In chapter 22 Dr. Dawson attempts to analyze the more obvi-
ous objections to his theory. To the criticism that it is too me-
chanical he answers that all life is essentially mechanical, *e. g.*,
respiration, circulation, menstruation. With the fact that the
majority of birds have only one ovary, yet the hen lays eggs of
both sexes, he has considerable trouble. But he makes argument
impossible by simply stating that woman is not analogous to the
hen. He seeks support for this contention by citing the fact that
birds are asymmetrical in other respects, *i. e.*, absence of right
carotid artery and right jugular vein, adding that it is ''no
more necessary to assume identity between birds and women in
the matter of the causation of sex, than in the matter of circu-
lation.'' It must be pointed out that originally (before hatch-
ing) both the circulatory and reproductive systems of birds are
identical, at least as concerns bilateral arrangement, with those
of the human embryo. It seems more reasonable, on the basis
of comparative embryology and physiology, that the human
ovaries have an identical, interchangeable and compensatory
function just as the kidneys, the testes, the eyes and the ovaries,
as respects menstruation, are known to have.

The two concluding chapters deal with the problem of fore-
casting sex and the production of sex at will. Knowing that the
gestation period is 40 weeks and that 13 ovulations normally

occur per annum and that the ovaries normally function alternately, one need know further merely the date of birth and sex of the previous child to compute the sex of the coming child. It is evident that the ovulation in the same months varies in successive years (due to the fact that there are 13 ovulations). From this point then we can work to the tenth month previous to the expected birth. Hence "if children are born in the same month an odd number of years apart they are of opposite sex; if an even number of years intervenes they are of the same sex" (p. 183). Accordingly then the "production of sex at will must consist in avoiding any attempt at fertilization in the months during which an ovum is produced of the sex not desired. Dr. Dawson believes it possible that some day by means of some modification of the Röntgen or other rays, we may actually see an ovary ovulate. At present there appears no way of determining the sex of the first-born.

The book as a whole furnishes entertaining and suggestive reading. One leaves it unconvinced, but stimulated perhaps to test the theory by careful observations of his own clinical materials. One feels, however, that the author is not justified in his extreme position that even higher vertebrates can teach us nothing with respect to the cause of sex and heredity in man. Surely one trained in general biology, especially cytology and comparative embryology can not accept the "theory" as anything more than an unverified hypothesis. Of course the array of clinical facts at first seems to give the theory a semblance of solidity; but this is rapidly dispelled by the arbitrary disposition made of numerous exceptions. By the same methods it would probably be as easy to prove the reverse position, *i. e.*, that females come from the right ovary and males from the left. The problem of sex can never be solved by the method of collecting clinical materials alone—and Dr. Dawson's book represents perhaps the last effort at such a solution. Clinical materials will always be valuable adjuncts, but the essence of sex resides probably as much in the male gametes as in the female, and its final elucidation seems indicated along the lines of a cytological (chromosomal?) interpretation of Mendelian phenomena.

<div align="right">H. E. JORDAN.</div>

INDEX

763